XVIII. On the Ocelli in the Genus Anthophorabia.

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SINCE the publication of my observations on the genus Anthophorabia, in the Transactions of the Society*, my attention has again been directed to the peculiarities exhibited by the principal organs of sense, and to the differences which exist in the comparative anatomy of these structures, the eyes, in the two sexes of insects of this genus. I now propose to offer a few remarks on the nature of these differences, in accordance with certain well-established laws in the anatomy and development of animals, and in extension of views which I have already begun to elucidate in the memoirs I have had the pleasure of communicating to this Society on the anatomy and development of Meloë.

On a former occasion† I pointed out the curious circumstance that the male individuals of this genus have occili at the sides of the head, instead of the large compound eyes which exist in the females, and other Hymenoptera, and that they have also three occili on the vertex. The existence of lateral occili in *Anthophorabia*, at precisely similar parts of the head as the compound eyes and occili in other insects, is incontrovertible, and yet it has been denied. It is equally certain that these structures, as I shall endeavour to show, are true representatives of organs of vision; and that, imperfect as they are, they are good generic distinctions.

The appearance which they exhibit under the microscope is, indeed, such as might readily induce those who are imperfectly acquainted with the laws of structural anatomy to regard them as merely coloured portions of the surface of the head, and not as ocelli, or organs of vision in any stage of development; and such observers might feel themselves supported in this opinion by the circumstance that there are also appearances on the cephalo-thorax of certain species of Arachnida, in the precise situation of ocelli in other species, which, by some, are regarded as mere spots or markings of the tegument, and not as the representatives of eyes.

This opinion would be fully entitled to respect, so long as its authors maintained it as an opinion, and made no attempt to enforce it in opposition to principles which are susceptible of demonstration, or to support it by supposed analogies.

To judge aright of the nature of the lateral ocelli, in the male *Anthophorabia*, we must not only remember that they correspond precisely, in situation, to the eyes in the female, but must also call to mind what are the essential conditions of a structure which is specially destined for the *appreciation of light*.

Professor Owen has stated ‡ that the lowest form of this structure in Fishes is—

^{*} Vol. xxi. pp. 63 & 79.

"a minute tegumentary folliele eoated by dark pigment, which receives the end of a special cerebral nerve," and he exemplifies this by reference to the eye of the Myxine and Lancelet, and also to that of the Amblyopsis spelæus*, a fish which constantly resides in the dark eaverns of Kentucky, and which at first was supposed to be completely eyeless, but which now is shown by Tellkampf † to possess eyes;—the fish, Amblyopsis, like the insect, Anthophorabia, having been misobserved in this respect, through imperfect investigation. The condition of the eye in these low forms of the organ in Fishes is very similar to that of the simple eyes in their lowest form in Insects. The eye of the insect, as long ago shown in my paper on Meloë, read to this Society, is, like all the external organs of its body, a tegumentary structure. It originates in a little eavity, pit, or simple depression, in the substance of the tegumentary portion of the head, which, lined with pigmentary substance, is more or less deep in proportion to the perfection of the organ, and it is eovered in on its exterior by a transparent portion of the external layer of tegument, which forms the cornea, and affords a free passage to light, which is received by the retina, or termination of a eerebral nerve at the base of the organ. This is the principle of construction, and the condition of the occllus, or simple eye in Anthophorabia (TAB. X. fig. 10 b, c), as in other insects. In the most perfect form of occllus in Insects, an iris and a lens also are present. The oeelli of the vertex, in Anthophorabia, are the most perfect in their structure (c). The cornea is quite transparent, nearly eircular in shape, and well-defined at its margins, as may be seen, with some care of manipulation, with the microscope; but it is much flattened, and forms only a very slight portion of a segment of a sphere. The choroid is deeply coloured, being formed of distinct pigmentary granules, which clothe the shallow eup-shaped eavity of the organ. The presence of this pigmentary choroid indicates the light-receiving function of the organ, but whether this organ be simply eapable of appreciating light, or whether also of distinguishing form, its focal length of vision must necessarily be very short, so that in this respect the facts of structure accord well with the observed and with the presumed habits of the insect.

The oeelli at the sides of the head (b) have the same general structure as those on the vertex, but are much more imperfect, in so far as respects the choroid; so that these oeelli may fairly be regarded as *simple appreciators of light*. The form of the cornea in these is an elongated oval, or lozenge-shape.

In all well-ascertained conditions of the simple eye in insects, the organ is found to contain, in addition to the parts mentioned, a concentrating refracting medium, a lens-like body, which is situated immediately behind the cornea, as was shown by Müller in the Arachnida‡. This lens-like body does, I believe, exist in the female *Anthophorabia*; but whether this structure, on which chiefly distinct vision and the power of the single eye of

^{*} Loc. cit.

[†] M. Th. G. Tellkampf in Müller's Archives for 1844, p. 381. See also fig. 50, p. 176, Owen's Lectures, 1846. Also the remark in Dr. F. H. Troschel's Report on Ichthyology for 1844, that the *Amblyopsis spelæus* "possesses minute eyes covered by the integument" (Ray Society, Reports on Zoology, 1847, p. 563). This is exactly what might be expected, seeing that, in all animals, the *cornea* is, originally, continuous with and forms part of the tegument.

[†] Physiol. des Gesichts-sinnes, p. 315. Annales des Sciences Naturelles, t. xvii. p. 232. Meckel's Archiv, 1829, pp. 38, 208.

distinguishing forms depend, exists in the most perfect of the eyes of the male, those of the vertex, I am not yet entirely satisfied. I have certainly detected appearances, in the nymph or pupa state of the male (fig. 10 b), which have led me to think that the *lens* is then present; but I have not satisfied myself of this in the perfect insect, and hence the appearances seen may have been due simply to the vitreous body, as it exists in some of the lower forms of the eye among the Annelida.

Whether, however, the lens does or does not exist, is of little importance with reference to the simple question as to whether these structures in the male *Anthophorabia* are the true homologues of the cyes in the female. That they are so I have not the slightest hesitation, after what I have shown, in affirming. The presence of a *cornea*, which covers a *chamber* lined with *pigment*, is sufficient proof to the physiologist and anatomist of the nature of the function of the structure.

The form of the cornea, however, shows that the field of vision is very limited. The cornea, as already stated, is but very slightly convex, being almost level with the surface of the head. This fact may have conducted some to the opinion that these are not visual organs. But neither the actual size of a simple eye, its form, nor the degree of its convexity, has any necessary connexion with the simple faculty of perceiving light. The convexity of the cornea has relation only to the extent of angle, or field of sight. The more convex, and the more elevated the eye is above the surface of the head, the greater proportion of a sphere does it necessarily include; and, as long ago shown by Prof. Müller, the greater the segment of a sphere formed by the eye, the greater is its expanse, or field of vision; while, on the contrary, the flatter or more depressed it is the more limited is this field, and the shallower the chamber the shorter is its focal distance.

The presence of the *lens* in the simple eye is essential to rendering the sight of images, and the appreciation of form, more or less perfect; and it does this in proportion to the more or less correct relation which it bears to other conditions coexistent with it.

With regard to the nerves supplied to these eyes, I may state that although I have not been able to trace those of the vertex so satisfactorily in the male Anthophorabia as I could have wished, owing to the numerous muscular fibres which run parallel to them, yet I have succeeded in tracing the optic nerve (d d) from the side of the cephalic ganglion, or rudimentary brain (d), transversely, in the direction of one of the lateral ocelli (b); and I believe, also, that I have distinguished the nerve which goes to the middle eye of the vertex (c). The nervous trunk which is given to the middle ocellus in Insects I have already shown, in my paper on $Pteronarcys^*$, is formed of two closely approximated nerves, one from each cephalic ganglion, as found by a careful dissection of that insect, and also of several Hymenoptera; and this probably is its condition in all other insects with three ocelli on the upper surface of the head.

I may here also refer to what is stated in my paper on *Meloë*[†], that there seems reason to think that in the Arachnida, and probably also in insects, the ocelli originate in the same way as the dermal tubercles, from which they appear to differ chiefly in the mode of development of their nuclei and nucleoli.

^{*} Linn. Trans. vol. xx. p. 440.

Further I may mention, with regard to the question concerning the eye-spots in the Arachnida, that I have found by dissection in the *Scorpionidæ*, not only that these are always situated in the exact place of eyes in other species, but also that they always receive a nervous filament from the same optic nerve which supplies the distinctly recognised organs of vision.

These facts, I trust, will be sufficient to show the general correctness of the description which I originally gave of the male *Anthophorabia*, that it is distinguished by the possession of ocelli, both at the sides of the head and on the vertex.

May 9, 1853.—To the foregoing remarks I may add a word on the condition of the eyes in the so-called blind Crustaceans from the caves of Kentucky. Distinct eyes exist both in Triura cavernicola and in Astacus pellucidus, Tellk. In Triura the eyes have very short pedicles, and are almost close together. In Astacus (fig. 11) they are partially concealed beneath the front of the head (b); their pedicles are conical, much shorter than in other species of the genus, and possess but little power of motion. The eye itself (fig. 12 and 13 b), although existing as a distinct structure, is destitute of a pigmentary choroid, in which respect it may be compared to the eye of the Albino. But the hardened tegument which clothes the entire organ is thinnest and most transparent in that part which forms the cornea (b) in other crustaceans; so that, although the eye may be unfitted for distinguishing form, the creature may yet possess the faculty of perceiving the small amount of actinic rays of light which penetrate into its subterranean abode. The cornea also exhibits an appearance of being divided into a few imperfect corneales at the apex of the organ (fig. 14), and the structure behind these into chambers, to which a small but distinct optic nerve is given (fig. 13 d d).

Probably other Articulata, which have been supposed to be entirely destitute of eyes, and, consequently, of the power of perceiving light, will be found to have the tegument which covers the place of the supposed lost organ thinner and more permeable to light there than in other parts. It seems fair to infer that this may prove to be the fact in all, from the already acknowledged susceptibility of some of the supposed eyeless insects to the presence of light; and also from the circumstance that in one of the Coleoptera, and in an Orthopterous insect, of the dark caves, Adelops hirtus and Phalangopsis ——?, the eye, as in others of the tribe, is distinctly indicated, as already shown by Tellkampf and by Thomson*. Hence we may fairly assume that the supposed eyeless Articulata differ from others of their class rather in the degree, than in the entire absence, of power of appreciating light.

^{*} Annals and Magazine of Natural History, vol. xiii. p. 112, No. 82. Feb. 1844.

EXPLANATION OF THE FIGURES.

TAB. X.

- Fig. 10. Front view of the head of the male Anthophorabia fasciata, highly magnified, and seen by transmitted light. A. The antenna, formed of ten joints, 1 to 10. b. The lateral, and c. the vertical ocelli. d. The rudimentary brain. dd. The optic nerve. e. The labrum. f. The mandibles. g. The labium. h. The maxillary palpi. i. The extensor, k. the flexor (?), and ll. the adductors of the antenna. m. The extensor, and n. the flexor of the distal joints of the antenna. o. The antennal nerve. p. The cosophageal ring. q. The subcosophageal ganglion, protected by r. the basilar apophyses of the head. s. The sub-epicranial apophyses, to which are attached, on their inner surface, the extensor of the antenna i, and on their external part of t. the extensor of the mandible. u. The flexor of the mandible. v. Extensor of the maxilla.
- Fig. 11. A young Astacus pellucidus from the caves of Kentucky, showing the presence of the eye (b).
- Fig. 12. Dissection of the cephalic portion of the young Astacus, by removal of the upper surface of the head, to show the distribution of optic nerves from the brain (d) to the eyes (b).
- Fig. 13. The eye, &c., highly magnified. a. Antennal nerves. b. The cornea. c. Brain. dd. Optic nerve.
- Fig. 14. Surface of the apex of the cornea, showing the rudimentary corneales.
- Fig. 15. The eye of Tallitrus locusta, showing distinct convex corneales; for comparison with Astacus.